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THE RÔLE OF THE GENUS RHAMNUS IN THE DISSEMINATION OF CROWN RUST.

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INTRODUCTION.

That certain species of Rhamnus, or buckthorn, may serve as the alternate hosts of crown rust (*Puccinia coronata* Corda) is well established through the excellent contributions of De Bary (*1*),[2] Klebahn (*7*), Eriksson (*3*), and others. The rôle that the alternate host may play in the dissemination and development of an epidemic of crown rust is not yet understood, however, because previous work had been confined largely to laboratory cultural studies. Until recently epidemiology studies have been impossible because of a lack of definite knowledge regarding the susceptibility of our American species of Rhamnus and their geographic range in the chief oat-growing sections of the United States.

As early as 1894 Henning (*5*) observed that *Rhamnus cathartica* L. was dangerous to oats because of its relation to crown rust. Some years later, in 1912, in response to repeated recommendations that *R. cathartica* be used as an ornamental shrub, Henning (*6*) stated that it should not be planted, citing Germany, Denmark, and Uruguay as examples of countries that have suffered epidemics of crown rust.

[1] The investigations of crown rust, of which the research covered by this bulletin is a portion, are conducted by the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture, in cooperation with the department of botany of the Iowa Agricultural Experiment Station. The writer wishes to express his thanks to Dr. I. E. Melhus, plant pathologist of the Iowa station, under whose immediate direction the investigation is conducted, for suggestions and criticisms during the progress of the work and the preparation of the manuscript; also to Miss Florence S. Willey, assistant pathologist at the Iowa station, and to the Office of Cereal Investigations, for assistance in gathering data and in arranging the material for publication.

[2] The serial numbers (italic) in parentheses refer to "Literature cited," at the end of this bulletin.

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Although crown rust is not of economic importance in Sweden, he suggested that *R. cathartica* might cause it to become so and recommended that this shrub be destroyed.

In America the literature on the rôle of Rhamnus in spreading crown rust has been confined to a few scattered observations. These observations, supplemented by recent cultural studies by Melhus, Dietz, and Willey (*8*), emphasized the necessity for a detailed study of this problem, including such phases as the distribution of the genus Rhamnus, the prevalence of æcidial infection, the dissemination of the æcidiospores, and the subsequent spread of uredospores. It is

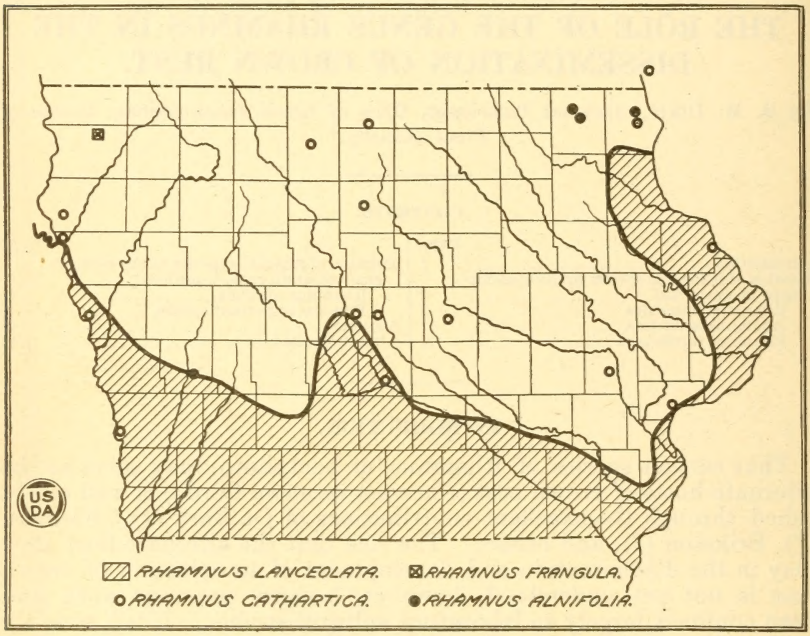

FIG. 1.—Sketch map of Iowa, showing the distribution of four species of Rhamnus, two native and two introduced.

the purpose in this bulletin to present data dealing with these phases of the problem.

RELATION OF RHAMNUS SPECIES TO THE EPIDEMIOLOGY OF CROWN RUST.

The part that Rhamnus species play in starting infections of crown rust has been studied by the writer during the past five years. Detailed studies have been made in Iowa throughout the season, from before any crown rust was present in the spring until the oats were harvested. These data have been substantiated by studies in the adjoining States of Minnesota, Wisconsin, Illinois, and Missouri and by periodical observations throughout the main sections of the United States in which species of Rhamnus occur. The distribution of native and introduced species of Rhamnus, or buckthorn, in Iowa is shown in Figure 1. These data are based on records obtained by the writer and his colleagues and by many other workers.

As there is considerable difference between the various species of buckthorn in regard to their behavior toward crown rust, each species will be discussed separately.

RHAMNUS CATHARTICA.

Rhamnus cathartica L. is indigenous to northern Asia and therefore is adapted to a cool climate. It is grown commonly throughout the North Central States as an ornamental shrub or hedge plant, under such popular names as buckthorn, hartshorn, rheinberry, and waythorn. Prior to the manufacture of barbed wire it was extensively planted in hedges as a substitute for fences. It was not a success as a fence, but, nevertheless, has found extensive use as an ornamental shrub.

The following places are the locations of some of the larger plantings of *R. cathartica* in Iowa (fig. 1): Boone, Clarion, Clinton, Council Bluffs, Des Moines, Dubuque, Forest City, Harlan, Hinton, Iowa City, Marshalltown, Monticello, Muscatine, Onawa, Whiting; and in Allamakee, Kossuth, and Pottawattamie Counties.

The general use of *R. cathartica* through a long period of time has afforded ample opportunity for it to escape into wood lots and waste lands. As this species bears abundant fruit each year it is probable that the birds and winds have been active agents in its distribution. Noteworthy occurrences of escaped shrubs have been found in Wisconsin, Minnesota, South Dakota, Illinois, and Iowa, often in close proximity to oat fields.

OCCURRENCE AT HINTON, IOWA.

In July, 1920, the attention of the writer was called by Dr. I. E. Melhus to a severe epidemic of crown rust at Hinton, Plymouth County, Iowa. This case was conspicuous because of the extent of the Rhamnus plantings and the numerous adjacent fields of oats. Northwest Iowa is fast becoming a chief oat-growing section of the upper Mississippi Valley. Out of 2,980 acres which were surveyed in detail in this locality, 1,020 acres were sown to oats. Many varieties were grown, the most common of which were Albion (Iowa 103), Richland (Iowa 105), Green Russian, and Silvermine. All of these varieties show some degree of susceptibility to crown rust.

An investigation of the cause of this epidemic was made, and a buckthorn hedge 520 rods long was found. An 80-acre farm in section 18 of Lincoln Township was completely surrounded by a hedge from 10 to 20 feet high, while the adjacent section 7 in the same township had about 80 rods of hedge. By questioning neighboring farmers it was learned that this hedge was planted about 50 years ago and that the oats grown near it had been severely rusted in many seasons. No definite data were obtainable for previous years, but in 1920, owing to an early epidemic of crown rust, the oat crop near the hedge was worthless. Indeed, much of the crop was not harvested because many of the plants did not head.

In 1921 a detailed study was made on the rate and distance of spread of crown rust from the infected Rhamnus shrubs in this hedge. The first pycnidia appeared on the leaves on May 13. The first æcidiospores were mature on May 16, and they were present in great abundance by May 17. From one to five æcidial cluster cups were

formed on each leaf, and many of the pedicels and fruits were completely covered with æcidia, which caused hypertrophy and subsequent falling. The leaves on the upper as well as lower branches were infected. On May 22 the first uredosori appeared on the oats growing within 70 feet of this hedge.

Previous to May 22 no crown rust had been found in any other part of Iowa within 40 miles of this farm surrounded by the Rhamnus hedge. In addition, oat fields were inspected along the Lincoln Highway from central Iowa to the western border and thence north to Hinton, but no uredosori were found. The first uredospores were found at Ames, Iowa, on June 4.

The percentages of rust infection were estimated on the basis of the scale in the agronomic notebook issued by the Office of Cereal Investigations of the Bureau of Plant Industry. Using one side of the field as a base line, perpendiculars were erected every 5 rods. Rust estimates were then made at approximately 5-rod intervals on these imaginary perpendiculars, and these percentages were recorded at the corresponding points on the map of this area. By this method an average of one rust reading was made for each 20 square rods. Each field of oats in the vicinity was studied in this way (fig. 2).

The spread of æcidiospores from this hedge during the 7-day period from May 22 to May 29 was determined by the apperance of uredosori on the oats in adjoining fields. The possibility of increase from the first uredospore generation to the second was excluded, as it requires fully seven days under average field conditions for one uredo generation to develop. The infection on oats from May 22, when the first uredo infection was found near this hedge, until May 29, therefore, was caused only by æcidiospores.

The hachured area in Figure 2 represents oat fields, and the intensity of the crosshatching is proportional to the degree of infection. A maximum infection of 85 per cent was evident on the oats adjoining the hedge, and the infection decreased in degree as the distance from the hedge increased. Additional oat fields were inspected at increasing distances from the hedge until not a trace of crown rust was found in the fields on the final date. Where only part of the area within a field boundary is hachured oats were growing in the entire field, but no infection was found in the areas which have no crosshatching. The infection in these outer fields usually was less than 1 per cent, and no infection was found during this period in the oat fields beyond the limits of the area represented in Figure 2, which covers 5 square miles.

The æcidiospores were dispersed in all directions, but chiefly toward the southwest; that is, a heavier infection was present on the oats southwest of the hedge, although the maximum distance to which infection was found in a southwesterly direction was but little greater than that in other directions. The maximum distance from the hedge at which æcidiospores caused infection was 452 rods, or nearly 1½ miles. It is probable that most of the æcidiospores were dropped within 5 rods of the hedge, as the highest percentage of infection was found within that distance. These data confirm an observation made by Eriksson (*4*), in which he suggests that the dispersal of spores from an infected buckthorn is rather limited.

Æcidiospores are mucilaginous, and it is most probable that they adhere to the first surface with which they come in contact, while

uredospores are dry and may be deposited and carried on a number of times before they are deposited finally and find favorable conditions for germination.

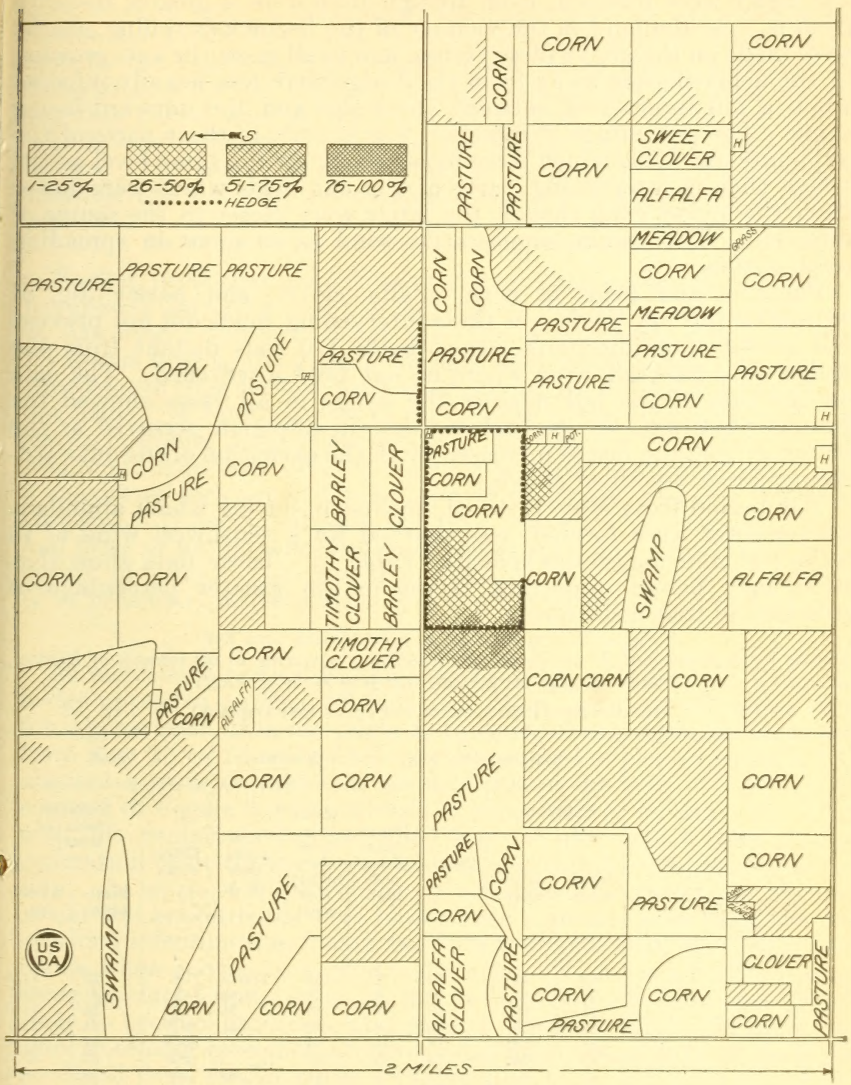

FIG. 2.—Sketch map of about 5 square miles surrounding the hedge of buckthorn (*Rhamnus cathartica*) near Hinton, Iowa, showing the location of oat fields and the percentage of uredospore infection caused by the spread of æcidiospores from the hedge from May 22 to 29, 1921. (Compare with fig. 4.)

FACTORS INFLUENCING THE SPREAD OF ÆCIDIOSPORES.

The degree of infection was influenced to some extent by the topography of the ground. In the oat field entirely surrounded by the hedge the grain in the ravines was more heavily infected than that on higher levels. The dew formed first in the ravines and remained there longer in the morning, which may partly explain the increased percentage of infection found there.

That the wind was an important factor in the spread of æcidiospores was suggested by the fact that oats growing on slopes inclined away from the hedge were not infected, while oats on slopes inclined toward the hedge were infected, even though they were a greater distance from it. As the land in the vicinity of the hedge was rolling, checks were made on the above observation, and in all cases the oats growing in the fields sloping away from the hedge were less heavily infected when a hill intervened between the hedge and the outward-facing slope. The percentage of infection was heavier in those parts of the adjoining oat fields which were most nearly on the same level as the hedge than in intervening parts of the oat fields which were lower than the hedge, even though the latter were closer to the source of infection. This, again, suggests the wind as an agent in spreading æcidiospores.

Pastures and fields of corn, alfalfa, clover, and barley (fig. 2) separated the oat fields, yet these intervening fields did not prevent the spread of æcidiospores, as oat fields 170 rods distant from the hedge were infected, even where no oat field intervened. The oats on the side of the hill nearest the hedge in all cases showed the heavier infection. A gradual decrease in infection occurred as the distance from the hedge increased, with the exception of the outward-facing slopes described above.

The period from May 19 to 21, inclusive, during which abundant æcidiospores were formed, was marked by a southwest wind of 48 miles per hour maximum velocity (Table 1). These data show that wind may be an important factor in the greater percentage of infection in that direction.

TABLE 1.—*Summary of the meteorological conditions occurring in the vicinity of Hinton, Iowa, during the period from May 16 to 31, 1921.*

[Relative humidities at 7 a. m. and 7 p. m. were averaged.]

Date.	Temperature (°F.).				Moisture.		Wind.		
	Extremes.		Mean.	Departure from normal.	Mean relative humidity (per cent).	Precipitation (in.).	Direction.	Velocity (miles per hour).	
	Maximum.	Minimum.						Maximum.	Average.
1921.									
May 16	63	42	52	9	59	Trace.	S	25	14.2
May 17	71	58	64	3	78	0.02	S	27	12.7
May 18	77	58	68	6	82	.26	S	25	14.0
May 19	80	59	70	8	80	.31	SW	48	22.1
May 20	87	64	76	14	61	.....	SW	32	18.1
May 21	87	69	78	15	63	.....	SW	32	21.0
May 22	89	65	77	14	61	.05	W	29	10.6
May 23	83	69	76	13	69	.....	N	12	7.4
May 24	82	65	74	10	79	.63	NE	25	13.4
May 25	83	64	74	10	76	.68	W	25	8.0
May 26	81	62	72	8	77	.79	N	22	6.2
May 27	80	61	70	6	70	.....	N	18	8.0
May 28	87	60	74	9	63	.....	SE	17	8.2
May 29	92	70	81	16	48	.....	S	29	12.2
May 30	78	61	70	5	83	.01	N	21	13.0
May 31	69	56	62	4	81	.....	E	18	10.1
Mean	82.2	61.4	71	8.6	70.6	.....	SW	.....	.....

The weather conditions shown in Table 1, which prevailed during the term when there was a major æcidiospore infection, were

favorable for dissemination and germination of the spores. The temperature, which averaged 8.6° F. above the normal for this period, was favorable to the germination of the æcidiospores. The first week in June usually marks the appearance of the æcidiospores under Iowa conditions, but their early appearance in 1921 may be due to the relatively high temperature during May. Infection was favored also by the high average relative humidity of 70.6 per cent for this period and the rainfalls on May 16, 17, 18, 19, 22, and 30, which were sufficient to moisten the foliage but not to wash off the spores. The heavy rains of May 24, 25, and 26 were sufficient to moisten the soil and keep a high relative humidity around the oat plants.

THE RÔLE OF GRASSES IN THE DISSEMINATION OF CROWN-RUST INFECTION.

Earlier investigations (*8*) have shown that crown rust of oats is capable of infecting many of our native grasses in the greenhouse. It has been a common belief that the æcidiospores fell from their Rhamnus host to the grasses beneath and caused infection and the uredospores thus formed were then carried by the wind to adjoining oat fields. A careful study of the grasses in the entire infected area shown in Figure 2 was made and only one, timothy (*Phleum pratense*), was found infected. Where growing beneath the hedge and within a maximun distance of 8 rods from it this host showed a few small rust sori. It is evident that the wild grasses of northwestern Iowa had little or no influence on the primary spread of crown rust in the spring of 1921. The principal grass of this district is bluegrass (*Poa pratensis*), which probably is not a host for crown rust of oats.

THE RATE AND DISTANCE OF UREDOSPORE DISSEMINATION.

As mentioned earlier, the first uredosori on oats near the Rhamnus hedge appeared on May 22, and as it takes from six to seven days for a generation of uredospores to mature, the infection in the period from May 22 to 28 represents only the spread of æcidiospores. This was not a gradual spread, as all oat fields in the area of 2,980 acres covered in Figure 2 were infected in some degree by May 23. This area then remained constant until May 28, after which time the first generation of uredospores was mature and capable of spreading infection. As no spore traps were set, it is impossible to ascertain whether or not the æcidiospores were blown over a greater area than the one in which infection was found, but it is probable that they were not viable when carried to a greater distance. Viable æcidiospores were being produced up to June 10, but as they had not been able previously to produce infection at a greater distance than 452 rods, the more extended spread of infection must have been due to uredospores produced from æcidiospores. (Table 2.)

TABLE 2.—*Rate of spread of crown rust to oats from a hedge of Rhamnus cathartica near Hinton, Iowa.*

Period.	Source of infection.	Area.	
		Acres.	Square miles.
May 22 to 28	Æcidiospore	2,980	5
May 29 to June 4	Uredospore	21,120	33
June 5 to 7	do	80,640	126
June 8 to 10	do	407,040	636

The six days from May 22 to 28 represent the term during which only æcidiospores caused infection. The remaining 13 days shown in Table 2 are the period in which the rapid spread was due to successive uredospore generations.

The direction and distance of infection in the period from June 5 to 7 are shown in Figure 3. The lack of infection southwest of Le Mars apparently is due to the fact that no oats were grown for several square miles. This area also is heavily wooded, and it may be possible that the trees offered some obstruction to the spread of the uredospores. In a detailed survey made of the area shown in Figure 3 no other specimens of Rhamnus were present than those in the hedge already described.

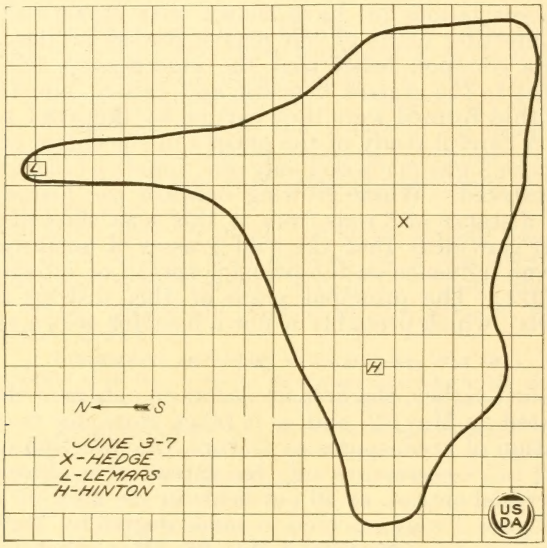

FIG. 3.—Sketch map of the district surrounding Hinton, Iowa, showing the spread of uredospore infection on oats at the end of June 7, by successive uredospore generations from the infected fields shown in Figure 2. The squares in the diagram represent square miles, and the heavy line is the outermost boundary of uredospore infection on that date.

On June 10 the infection was traced to a maximum distance of 53 miles from the hedge. The spread of infection after this time was too rapid and covered too much territory to be followed by the survey.

The destructiveness of this epidemic is shown in Figure 4, which represents the conditions on June 7 in the same area and drawn to the same scale as Figure 2. In comparing Figures 2 and 4 it will be noticed that the heaviest infection is located in the same relative place in each, showing that the areas of heaviest primary infection maintained a relatively higher infection throughout the season. The oats in the fields adjoining the hedge were a total loss (figs. 5 and 6) and were not harvested. The yields were small on the entire 1,020 acres comprising the oat acreage in this area, the kernels were light, and a relatively small percentage of the crop was of marketable grade.

From the studies made it became evident that this hedge was a menace to oat production in northwestern Iowa and probably northward into South Dakota and Minnesota. The farmers of this com-

munity in northwestern Iowa realize the harmful effects of the Rhamnus hedge and up to the present time have dug up 240 rods of it (fig. 7). This eradication has been accomplished by means of a stump puller, which removes the bushes but allows the soil to remain

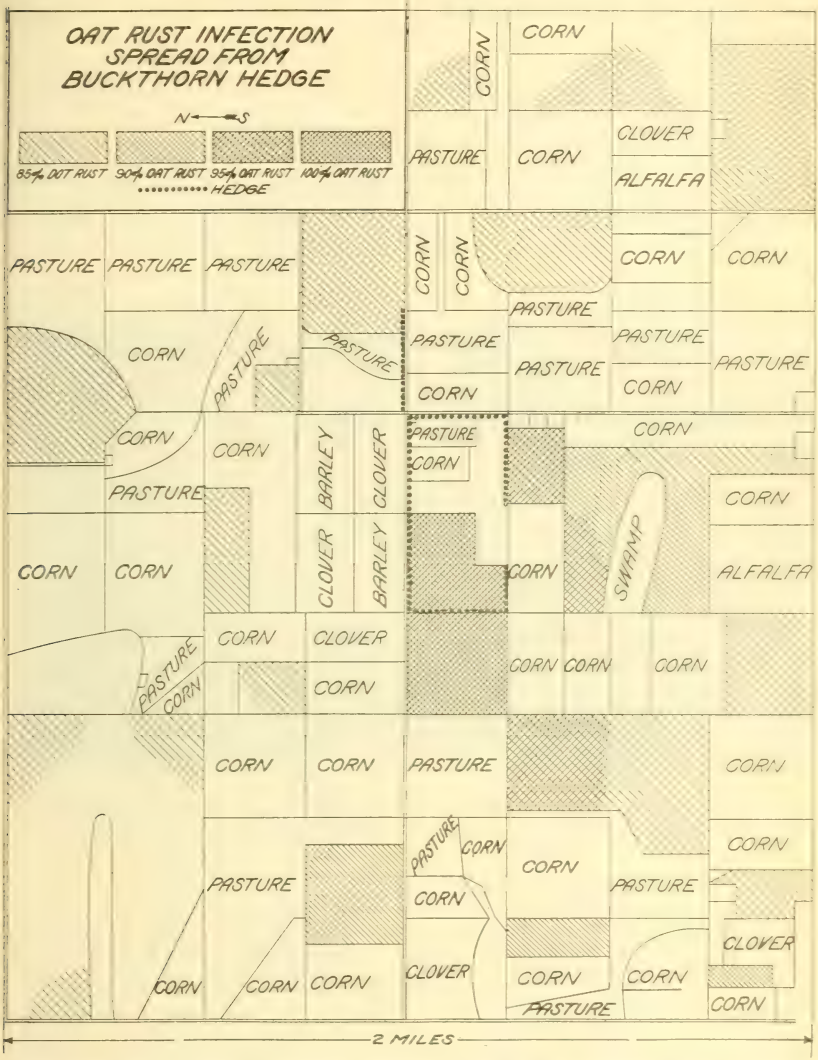

FIG. 4.—Sketch map of about 5 square miles surrounding the hedge of buckthorn (*Rhamnus cathartica*) near Hinton, Iowa, showing the location of the oat fields and the percentage of infection which had occurred to the end of June 7. (Compare with fig. 2.)

around the roots. Unless this soil is removed, the plant will continue to live and put out leaves, and these may bear heavy æcidial infection. However, the shrubs pulled in this way seldom survive until the second spring after being removed.

OTHER EPIDEMICS.

A 10-acre pasture at Clarion, Iowa, in which *Rhamnus cathartica* has escaped from cultivation, has been under observation for the past three years, although it was not studied in as much detail as the planting at Hinton. The cultivated shrubs were 10 to 20 feet high, and the escaped shrubs ranged from mere seedlings to a height of 4 feet. During this 3-year period both the cultivated and escaped shrubs have borne æcidial infection, although only a maximum infection of 10 per cent occurred on any of the shrubs. In the spring of 1921 a more detailed study was made of this area. The æcidial stage appeared on the Rhamnus leaves previous to the advent of the uredospore stage on oats. The oats adjoining the hedge showed the first crown rust infection in this locality. The oats in the portion of the field farthest removed from the hedge developed the least infection. All evidence

FIG. 5.—Hedge of *Rhamnus cathartica* near Hinton, Iowa. The oats adjoining this hedge had 100 per cent of crown-rust infection. The crop was barely knee high, many plants not heading. The yield from this field did not pay the expense of harvesting. Photographed July 1, 1921.

pointed to the fact that *R. cathartica* acting as an alternate host caused the initial infection of crown rust on these oats.

In August, 1919, and in July, 1920, and July, 1921, several oat fields were inspected in the vicinity of Janesville, Avalon, Emerald Grove, and Delavan Lake, Wis., where many shrubs of *R. cathartica* have escaped from cultivation. Hedges were found along the roadsides, and seedlings were scattered throughout the vicinity. During the springs of 1919 and 1921 the æcidial infection was so severe that the shrubs were entirely defoliated. In 1919 the oats in the fields adjoining the buckthorns were not worth cutting. The oats inspected within a 2-mile radius were severely injured. In 1920 the æcidial stage was again present on the bushes, and this infection was disseminated to oats. The next year, 1921, witnessed another severe loss in the yield of oats which was traceable to infection from the neighboring buckthorn shrubs.

Æcidiospores have been collected on *R. cathartica* in the vicinity of Madison, Wis., during the past four years, and each year the oats adjoining the hedges have been heavily infected.

The rôle played by *R. cathartica* was demonstrated also at Warren, Minn., by Dr. Henry S. Conard, of Grinnell, Iowa, in July, 1919. A few weeks later further investigations were made at Warren, where 15

FIG. 6.—Two samples of oats from different parts of the same field. The right-hand sample, showing 100 per cent infection with crown rust, was cut adjoining the hedge shown in figures 5 and 7. The left-hand sample came from the distant side of the same field. The intervening oats showed a gradual decrease in percentage of infection and increase in height and size of panicle as the distance from the hedge increased. Photographed July 1, 1921.

hedges of *R. cathartica* were studied. The field of oats nearest to a hedge was about half a mile distant. The rust infection in this field was 90 per cent. Every field of oats inspected within a radius of 10 miles was heavily infected with crown rust. Teleutospores were developing on the oats nearest the hedges, while the rust on the oats farther away was only in the uredospore stage. The county agent

at Warren reported that the owners of these hedges had sent him many samples of buckthorn leaves heavily infected with the æcidial stage of crown rust during the spring of 1919.

Additional observations have been made at Fargo, N. Dak., Antioch and Freeport, Ill., and Duluth, Minn., where *R. cathartica* has caused local epidemics of crown rust.

RHAMNUS LANCEOLATA.

Although unknown in the Old World, *Rhamnus lanceolata* Pursh is perhaps the most widely distributed native species. It is commonly known as lance-leaved buckthorn and grows most commonly along narrow streams and shaded dry runs. Its range extends from eastern

FIG. 7.—Plants of *Rhamnus cathartica* from the hedge shown in figure 5. The great lumps of dirt left on the roots by the stump puller enabled the plants to remain alive. They produced leaves in the spring, and these had abundant æcidial infection. Photographed July 1, 1921.

Nebraska and through central Iowa eastward to Pennsylvania and southward to Florida. This shrub has been collected from the following places in Iowa (see fig. 1): Adel, Bellevue, Bloomfield, Centerville, Council Bluffs, Dubuque, Elkader, Indianola, Le Claire, Monmouth, Morning Sun, Mount Pleasant, Osceola, Oskaloosa, Ottumwa, Postville, Salem, Sioux City, Volga, Winterset; also at "The Ledges" in Boone County, in Decatur County, in the north side of Marion County, in Shelby County, and along the South River in Warren County. It is not frequently found adjoining oat fields.

STUDIES IN IOWA.

As *R. lanceolata* is one of the most widely distributed native species it is important to know to what extent it bears the æcidial stage of

crown rust and whether or not it is instrumental in starting the initial infection on oats and other grasses. The situation has been studied in detail in Iowa, and many observations have been made throughout the region in which this shrub grows. The principal studies were carried on near Indianola, as this town is located about in the center of the area in which *R. lanceolata* occurs in Iowa. These studies were further substantiated by observations at Bloomfield and Osceola.

Each spring since 1917 field observations have been made on *R. lanceolata* in the vicinity of Indianola to ascertain its relation to a yearly infection of crown rust on oats. Æcidial infection was found on these shrubs every year. However, the maximum infection, in 1919, showed only 10 per cent of the leaves bearing æcidia. When the berries were infected the æcidial cups covered the entire fruit and often the pedicel. These shrubs, which varied from mere seedlings

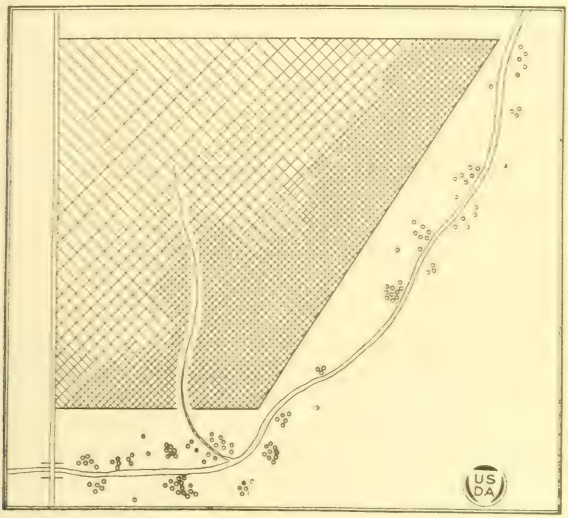

FIG. 8.—Sketch map of an oat field and adjacent shrubs of *Rhamnus lanceolata* near Indianola, Iowa, showing the spread of uredospores from æcidiospores, causing an infection of 15 per cent on the oats nearest the shrubs, with gradually diminishing infection to less than 1 per cent at the distant side of the field.

to trees 15 feet high, bore æcidia on the topmost leaves as well as on those near the ground.

Observations also were made in a locality 3½ miles southwest of Indianola, where, along the banks of a small stream, hundreds of seedlings as well as mature plants were found. This stream flows along a 90-acre field which was sown to oats in 1919. Shrubs bearing æcidia grew within 100 feet of this field. An infection of 15 per cent occurred on the oats nearest the shrubs, with a gradually diminishing infection at greater distances until only a trace or less than 1 per cent was found in the most distant portions of the field. (Fig. 8.) This field had a southeastern exposure toward the bordering stream. The area showing the heaviest infection also was most favored by heavy dews, which fall earlier in the evening and remain longer in the morning, thus providing more favorable conditions for infection

to develop in the area nearest the buckthorns. Numerous grasses bordered this area, though *Phleum pratense* L. and *Calamagrostis canadensis* (Michx.) Beauv. were the only two grasses which were infected with crown rust. The flora directly beneath the Rhamnus shrubs consisted largely of sedges.

At still another location, about 7 miles removed from this field *Phleum pratense*, *Calamagrostis canadensis*, *Sphenopolis* (*Eatonia*) *obtusata* (Michx.) Scribn., *Agrostis hyemalis* (Walt.) B. S. P., and *Avena sativa* L. were infected with crown rust when growing near *Rhamnus lanceolata*. In addition, *Festuca elatior* L. was found infected with crown rust in 1921. Although many cases have been inspected during the past five years, that at Indianola in 1919 is the only one which gave positive evidence that *R. lanceolata* is instrumental in spreading the crown rust to oats under field conditions.

Although æcidial infection occurs on this species at Osceola and at Bloomfield, Iowa, each year, the situation at the latter place is different from those previously discussed. At Bloomfield, which is in the extreme southern portion of the State, H. H. Plagge found uredospore infection on oats in 1919 previous to the appearance of æcidial infection on *R. lanceolata*. It is probable that crown rust here had hibernated as mycelium or in the uredospore stage, a rare occurrence in Iowa.

R. lanceolata is not used as a hedge or ornamental shrub and therefore is seldom found growing in the immediate vicinity of oat fields. It should be noted also that the area comprising the habitat of this shrub lies principally outside the main oat-growing section of the Middle West.

STUDIES IN ARKANSAS AND MISSOURI.

From April 2 to 10, 1919, an extensive field study was made in the vicinities of Fort Smith, Prescott, and Little Rock, Ark., to determine whether this shrub was instrumental in starting the annual infection of crown rust in that section. At this time *R. lanceolata* was just coming into leaf and no infection was evident, although uredosori were common on winter oats. As crown rust often lives over winter in Arkansas, this shrub seems to play only a minor rôle in the initial appearance and subsequent dissemination of crown rust there.

Æcidial infection occurs on *R. lanceolata* in Missouri annually, as shown by studies at Arlington. It was not found infected at Mountain Grove, in the southern part of the State, during the springs of 1919 and 1920. Here, as in Iowa, the shrub seldom grows near oat fields, and hence its opportunity for aiding the spread of crown rust is not extensive.

RHAMNUS CAROLINIANA.

Rhamnus caroliniana Walter is a native species extending eastward from Texas, Kansas, and Missouri, the latter State being the northern limit of its range. It is abundant on shaded hillsides and stony ridges of eastern Kentucky and Tennessee. It most closely resembles *R. lanceolata*, which it largely supplants in the southeastern section of the United States.

The hills surrounding Knoxville, Tenn., bear an abundant growth of this shrub, varying in height from 6 inches to 30 feet or more.

Observations made in April, 1919, just as these shrubs were coming into leaf, showed no evidence of infection. Oats growing in an adjoining field showed no uredospore infection. In July, however, this field was heavily infected with crown rust, although there still was no trace of æcidial infection on the Rhamnus. Carl Kurtzweil reported æcidial infection on Rhamnus at this location in 1920.

Observations were made at Lexington, Ky., and in the Missouri Botanical Garden at St. Louis in 1919, but no æcidial infection was present. Dr. Harrison Garman, in a personal conversation, said that *R. caroliniana* was heavily infected at Lexington, Ky., and Arthur reported finding æcidia on *R. caroliniana* in a garden at La Fayette, Ind., in 1905. Although repeated search has been made, the writer has never found æcidia on this shrub in the field. Plantings on the campus at Ames, Iowa, have never developed æcidiospores, though oats heavily infected with crown rust grew near the Rhamnus.

Greenhouse experiments in which teleutospores from *Avena sativa* were used as inoculum gave only pycnidia (*8*). However, in the spring of 1922 a few cluster cups were formed on *R. caroliniana* in the greenhouse trials with the teleutospores from *Avena sativa*.

Because of the limited investigations made, the rôle of *R. caroliniana* in spreading crown rust of oats is thus far not well understood. The data available suggest that it is not an important alternate host for the specialized form of crown rust occurring on the cultivated oat.

RHAMNUS ALNIFOLIA.

Rhamnus alnifolia L'Her., or dwarf alder, which is largely confined to swamps and shaded banks of streams, is primarily a northern species, reaching the southern limits of its distribution in the northern portions of Iowa, Nebraska, and Illinois. In Iowa it has been collected at Decorah and along the Yellow River in the northeastern part of the State. It grows abundantly also in Door county, in northeastern Wisconsin. About 25 oat fields were inspected in that county, but crown-rust infection was almost entirely absent. A maximum infection of 10 per cent was found, but this was confined to a few small local patches.

In the lowlands surrounding Sturgeon Bay, Wis., *R. alnifolia* grows in great profusion. The grass flora of this locality consists mostly of *Calamagrostis canadensis*, which occurs beneath these shrubs and often extends to the edge of the lowlands where oats are grown. This locality has been under observation for the past four years to determine the possible relationship between the æcidial infection on this buckthorn and the uredospore infection on oats. Abundant teleutospore and uredospore material on Calamagrostis has been collected there in every year except 1920, when the infection was light.

On May 24, 1919, *Calamagrostis canadensis* infected with uredospores of crown rust was growing in the vicinity of *R. alnifolia* at Sturgeon Bay, Wis. The Rhamnus at this time was just coming into leaf and showed no traces of infection. Greenhouse tests (*8*) have shown that crown rust on *C. canadensis* is only occasionally able to infect oats. Although it was evident that æcidia on *R. alnifolia* were directly responsible for infection on Calamagrostis, this buckthorn probably does not act as a direct agent in the distribution of crown rust to oats.

FIVE LESS IMPORTANT SPECIES.

Various factors and combinations of factors cause *Rhamnus frangula*, *R. smithii*, *R. purshiana*, *R. californica*, and *R. crocea* to be less important in the dissemination of crown rust to oats than are the species previously mentioned. These species of Rhamnus have a limited distribution and their habitats lie principally outside of the oat-producing sections. They frequently are found at high altitudes, far removed from cultivated fields, which precludes the possibility of their becoming infected under ordinary field conditions.

RHAMNUS FRANGULA.

Rhamnus frangula L., commonly known as black alder, berry alder, and arrowwood, is a native of Europe. It often is used in the United States as a hedge and ornamental plant and has escaped commonly in bogs and wet places on Long Island, in northern New Jersey, and in Ontario, Canada, according to Britton (*2*). It is not common in the Middle West, but has been reported by J. B. Mayer as escaped from cultivation at Hull, Iowa, which is the only place known to the writer where *R. frangula* occurs as an escape in Iowa.

According to greenhouse trials (*8*) *R. frangula* developed pycnidial infection, but never æcidial infection, when exposed to teleutospores from species of Avena and Calamagrostis, two of the most widely distributed crown-rust hosts in the oat-producing region. The escaped plants near Hull in the northwestern part of the State and cultivated plants at the Missouri Botanical Garden in St. Louis both have been inspected, but there was no æcidial infection at either place. Although but limited observations have been made, it seems probable that *R. frangula* is of little importance in the dissemination of crown rust in the Middle West.

RHAMNUS SMITHII.

Rhamnus smithii Greene, a thick-stemmed dwarf shrub bearing lanceolate leaves, is confined to a few thousand acres near Pagosa Springs in southwestern Colorado, where it grows very abundantly. It is rarely found near cultivated fields. It is cultivated in Boulder, Colo., where it thrives and often reaches a height of 12 feet.

At Pagosa Springs, Colo., a relatively high percentage of æcidial infection was present in 1920 and 1921.

Teleutospores of crown rust were collected at that place on *Agropyron smithii*, *Koeleria cristata*, *Bromus ciliatus*, and *Trisetum* sp. by Miss Florence Willey in July, 1921. Shrubs of *R. smithii* growing near these grasses were heavily infected. Later in the season uredospores were collected on *Bromus* sp. growing beneath heavily infected bushes. Although the relationship of this alternate host to these grass species must be verified by controlled greenhouse study, it is probable that it is not of much importance in spreading crown rust to oats, as little of this cereal is grown in the vicinity. Its response to infection with teleutospores from oats under greenhouse conditions (*8*) suggests its close relationship to *R. lanceolata*. It may be that *R. smithii* is only a form of *R. lanceolata* which has become adapted to the high altitudes of the Rocky Mountain region.

RHAMNUS PURSHIANA.

Rhamnus purshiana DC. is a western species occurring commonly in California, Oregon, Washington, Idaho, and Montana. Its natural habitat is at an elevation where cultivated fields do not occur.

Although *R. purshiana* has been infected with the æcidial stage of crown rust in the greenhouse, it probably is not a source of infection in oats, as it grows at high altitudes in the mountains while oats are grown in the valleys.

RHAMNUS CALIFORNICA.

This species and the variety *tomentella* are largely confined to the western coast of the United States. The field observations on *Rhamnus californica* Esch. are limited, but probably it plays little or no part in the spread of crown rust to oats. It grows in a warm temperate climate where the uredospore stage of crown rust exists throughout the entire year.

RHAMNUS CROCEA.

Experiments (*8*) have shown that *Rhamnus crocea* Nutt. will produce æcidiospores when exposed to infection with teleutospores obtained from *Calamagrostis canadensis*. The results of experiments conducted in 1922 gave a like degree of infection with teleutospores from *Festuca elatior* and *Avena sativa*. These data indicate that this species might be able to play an important rôle in the spread of crown rust to oats. However, *R. crocea* is limited to a small area in southern California and to certain islands off the coast and is unimportant because it commonly does not occur within an oat-producing area.

SUMMARY.

Rhamnus cathartica L., a native of Asia, has long been used as an ornamental shrub in this country and has escaped commonly into wood lots and waste lands throughout the north-central and northeastern United States.

This shrub commonly bears æcidia of crown rust (*Puccinia coronata* Corda), and was found to be the cause of severe epidemics of crown-rust in Iowa, Wisconsin, Minnesota, and Illinois.

The epidemic at Hinton, Iowa, caused by æcidial infection on a 520-rod hedge, was so severe in 1921 that the oats in adjoining fields were not harvested.

Topography, wind, and other climatic conditions during the time the æcidiospores are forming probably are the most important factors in the spread of crown rust. Wild or cultivated grasses growing near the infected hedge apparently had little influence on the spread of the rust.

Æcidiospores from *R. cathartica* caused infection to a distance of 452 rods, or nearly 1½ miles, in seven days, or before the first uredospores were ripe. The infection was heavy near the hedge and progressively lighter as the distance from it increased. After the first generation of uredospores was mature, the spread of infection was very rapid. Thirteen days later oats were infected at a maximum distance of 53 miles from the hedge.

Rhamnus lanceolata Pursh is perhaps the most widely distributed native species. It occurs commonly from eastern Nebraska across south-central Iowa to Pennsylvania and southward to Florida. It is not used as an ornamental shrub and seldom grows near cultivated fields. Though it bears æcidia every year, the case at Indianola, Iowa, is the only one known to the writer where this species was responsible for the initial infection of crown rust of oats.

Æcidiospores collected on *R. lanceolata* were capable of infecting *Phleum pratense*, *Calamagrostis canadensis*, *Agrostis hyemalis*, and *Festuca elatior* under field conditions. As uredospores overwinter in the South, it is probable that this species plays little part in the initial infection by crown rust there.

Rhamnus caroliniana is another native species, extending eastward from Texas, Kansas, and Missouri to the Atlantic coast. Apparently it does not bear æcidiospores every year, but in recent greenhouse experiments cluster cups were produced when it was exposed to infection by teleutospores from oats. *R. alnifolia* is a native northern species bearing heavy æcidiospore infection of crown rust where *Calamagrostis canadensis* grows near it. Although it has been found to aid the spread of crown rust to this grass, no case is known where it was a factor in spreading the specialized form of crown rust which occurs on oats.

Five other species of buckthorn, one introduced and four native, namely, *R. frangula*, *R. smithii*, *R. purshiana*, *R. californica*, and *R. crocea*, are relatively unimportant in the dissemination of crown rust to oats. *R. frangula* has escaped from cultivation in the northeastern United States.

The others are species of very limited distribution in the far West and usually distant from fields of oats. *R. smithii* and *R. purshiana* bear æcidia under field conditions, and grasses near the former species become infected.

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